Report

Current Biology

The Evolution of Lateralization in Group Hunting Sailfish

Highlights

- Sailfish show individual-level attack lateralization when attacking their prey
- More strongly lateralized individuals had a higher capture success
- Sailfish bills showed one-sided teeth abrasions
- Predictability of attack direction decreased with increasing sailfish group size

Authors

Ralf H.J.M. Kurvers, Stefan Krause, Paul E. Viblanc, ..., Pierre Couillaud, Kevin M. Boswell, Jens Krause

Correspondence

kurvers@mpib-berlin.mpg.de

In Brief

Kurvers et al. discovered that sailfish show individual-level attack lateralization when attacking schooling prey. More strongly lateralized sailfish had a higher capture success. Whereas single sailfish are highly predictable to their prey due to attack lateralization, groups are highly unpredictable, identifying a novel benefit of group hunting.

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The Evolution of Lateralization in Group Hunting Sailfish

Ralf H.J.M. Kurvers,[1,2,13,*] Stefan Krause,[3] Paul E. Viblanc,[2,12] James E. Herbert-Read,[4,5] Paul Zaslansky,[6] Paolo Domenici,[7] Stefano Marras,[7] John F. Steffensen,[8] Morten B.S. Svendsen,[8] Alexander D.M. Wilson,[9] Pierre Couillaud,[10] Kevin M. Boswell,[11] and Jens Krause[2,12]

[1]Center for Adaptive Rationality, Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany
[2]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Mueggelseedamm 310, 12587 Berlin, Germany
[3]Department of Electrical Engineering and Computer Science, Lübeck University of Applied Sciences, 23562 Lübeck, Germany
[4]Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden
[5]Department of Mathematics, Uppsala University, 751 05 Uppsala, Sweden
[6]Julius Wolff Institut, Charité - Universitätsmedizin Berlin, Föhrer Str. 15, 13353 Berlin, Germany
[7]IAMC-CNR, Istituto per l'Ambiente Marino Costiero, Consiglio Nazionale delle Ricerche, Località Sa Mardini, 09170 Torregrande, Oristano, Italy
[8]Marine Biological Section, Department of Biology, University of Copenhagen, Strandpromenaden 5, 3000 Helsingør, Denmark
[9]School of Life and Environmental Sciences, University of Sydney, Heydon-Laurence Building A08, Sydney, NSW 2006, Australia
[10]Département du Master Sciences de l'Univers, Environnement, Écologie, Université Pierre et Marie Curie, 4 Place Jussieu, 75005 Paris, France
[11]Department of Biological Sciences, Florida International University, 3000 N.E. 151st Street, North Miami, FL 33181, USA
[12]Faculty of Life Sciences, Albrecht Daniel Thaer-Institut, Humboldt-Universität zu Berlin, Invalidenstrasse 42, 10115 Berlin, Germany
[13]Lead Contact
*Correspondence: kurvers@mpib-berlin.mpg.de
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SUMMARY

Lateralization is widespread throughout the animal kingdom [1–7] and can increase task efficiency via shortening reaction times and saving on neural tissue [8–16]. However, lateralization might be costly because it increases predictability [17–21]. In predator-prey interactions, for example, predators might increase capture success because of specialization in a lateralized attack, but at the cost of increased predictability to their prey, constraining the evolution of lateralization. One unexplored mechanism for evading such costs is group hunting: this would allow individual-level specialization, while still allowing for group-level unpredictability. We investigated this mechanism in group hunting sailfish, *Istiophorus platypterus*, attacking schooling sardines, *Sardinella aurita*. During these attacks, sailfish alternate in attacking the prey using their elongated bills to slash or tap the prey [22–24]. This rapid bill movement is either leftward or rightward. Using behavioral observations of identifiable individual sailfish hunting in groups, we provide evidence for individual-level attack lateralization in sailfish. More strongly lateralized individuals had a higher capture success. Further evidence of lateralization comes from morphological analyses of sailfish bills that show strong evidence of one-sided micro-teeth abrasions. Finally, we show that attacks by single sailfish are indeed highly predictable, but predictability rapidly declines with increasing group size because of a lack of population-level lateralization. Our results present a novel benefit of group hunting: by alternating attacks, individual-level attack lateralization can evolve, without the negative consequences of individual-level predictability. More generally, our results suggest that group hunting in predators might provide more suitable conditions for the evolution of strategy diversity compared to solitary life.

RESULTS

Behavioral Observations

Under snorkel, we filmed sailfish groups attacking schooling sardines (range school size: 35∼1,000), 30–70 km offshore of Cancun using handheld cameras (Casio EX-FH100 and HD GOPRO HERO 3) over the course of 3 years (January to March 2011–2013). During these group hunts, sailfish alternate attacking the sardines, which continuously attempt to evade predation [22, 23]. Sailfish use their elongated bills to either slash or tap the prey [22], which occurs with a distinct leftward or rightward movement (Movies S1, S2, and S3). These hunts can last several hours.

For each sailfish group (n = 11, range group size: 1–14), we created a database with images of all the different sailfish (n = 73), using close-ups of the dorsal fin whose shape is unique for each individual (Figure 1). Occasionally, we also used broken bills or obvious body scars as additional identifiers. For all attacks we filmed (n = 365), we determined the identity of the attacker, whether the attack movement was

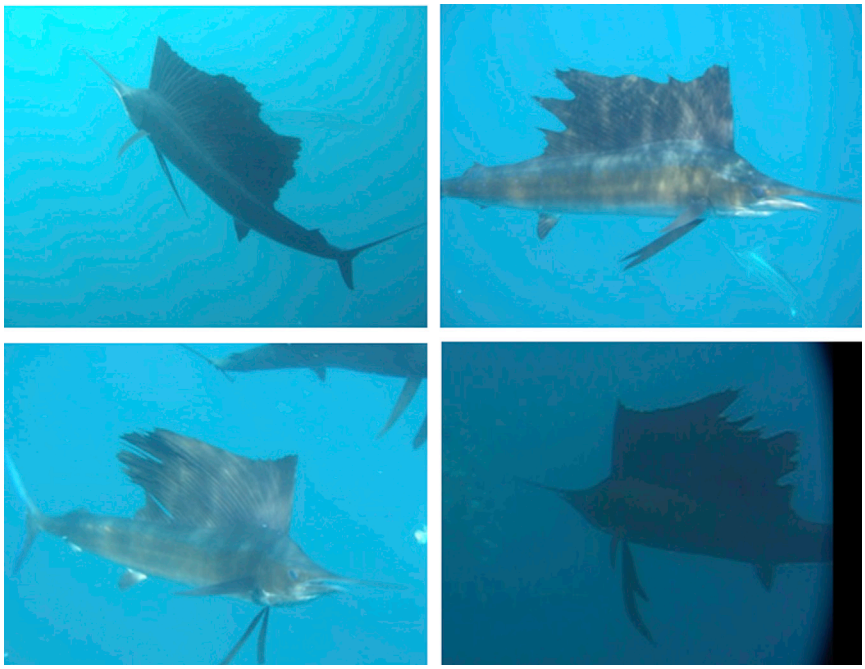

Figure 1. Identification of Individual Sailfish
Images of four different sailfish, illustrating how individuals can be identified by the unique patterns of their sails.

leftward or rightward, and whether the attack resulted in successful prey capture (inter-rater agreement was high for both attack direction and capture; see Supplemental Experimental Procedures). Figure S1A shows the number of observed attacks per sailfish. Individuals that were observed only once or twice (n = 28) were excluded from all analyses. For all remaining sailfish, we then calculated their laterality index (LI) using (LA – RA)/(LA + RA), where LA is the number of leftward attacks and RA the number of rightward attacks, and compared the observed LI distribution to the expected LI distribution assuming no individual lateralization, using a chi-square test. The observed LI frequencies differed significantly from the expected LIs (Figures 2A–2F; all $p < 0.01$). At low absolute LI values (i.e., $|LI|$), the observed frequencies were lower than expected, whereas at intermediate to high absolute LI values, the observed frequencies were higher than the expected distribution, providing strong evidence for lateralization of attacks in individual sailfish. The number of times an individual sailfish was observed did not affect its absolute LI (Figure S1B).

Next, we investigated whether the strength of lateralization affected an individual's capture success, only including sailfish for which we observed at least three attacks (n = 45 sailfish, 320 attacks, mean number of attacks per sailfish: 7.11, range: 3–20). There was a positive relationship between an individual's absolute LI and capture success (generalized linear mixed model: Est. ± SE = 1.91 ± 0.79, z = 2.42, p = 0.015; Figure 3A; see Supplemental Experimental Procedures for statistical procedures), suggesting that individuals that were more strongly lateralized had higher capture success than individuals that were weakly lateralized. Moreover, sailfish had a higher capture success when attacking with their preferred side (i.e., the side they used most often; see also Figure S1B) than when attacking with their non-preferred side (1.38 ± 0.62, z = 2.22, p = 0.027; Figure 3B). The difference in capture success between the preferred and non-preferred side increased with increasing LI: the stronger individuals were lateralized, the more successful they became when using their preferred side relative to using their non-preferred side (0.25 ± 0.10, t = 2.43, p = 0.022; Figure 3C). When including only sailfish for which we observed at least four or five attacks, we observed similar results (Figure S2). There was no significant difference in capture success between sailfish that attacked predominantly leftward (n = 19) and sailfish that predominantly attacked rightward (n = 19), and both "types" were present in equal numbers (Figure S3), suggesting that there is no population-level lateralization (see also Figures 2A, 2C, and 2E).

Morphological Measurements

Sailfish bills are covered laterally in micro-teeth ([25, 26]; Figure 2G), and when sailfish attack, these micro-teeth make contact with the sardines causing injuries including scale and tissue removal [22]. Tooth wear has been used for aging and inferring dietary habits in different species [27, 28], and here we investigated whether there was evidence for asymmetrical tooth wear, which might indicate behavioral lateralization of bill use. This idea is supported by evidence from medical investigations that show that in humans, the dominant hand gets injured more often than the non-dominant one [29]. We obtained 12 sailfish bills from the Cancun area and Reunion Island. For each bill, we analyzed the first 5 cm where biomechanical forces during slashing are greatest [22]. For each bill-tip, we created a negative impression using Dental Milestones Guaranteed Honigum light dental impression material. Negative impressions were digitalized using a desktop scanner and transformed into binary images using ImageJ, whereby the micro-teeth appear as black dots on the binary images of the dental impressions. We subdivided each image length-wise into 20 equal sections of 2.5 mm and then used particle analyses in ImageJ to calculate the number of micro-teeth exceeding 0.2 mm in base width on the left and right side of the bill per section (see Figure S4 for the distribution of micro-teeth on the left and right side of each bill). For each bill-tip, we then tested whether there were significantly more micro-teeth on one side of the bill compared to the other, using a paired t test. From the 12 bill-tips, three had significantly more micro-teeth on the left side than the right side ($p < 0.05$), seven had significantly more micro-teeth on the right side than the left side ($p < 0.05$), and two had no significant

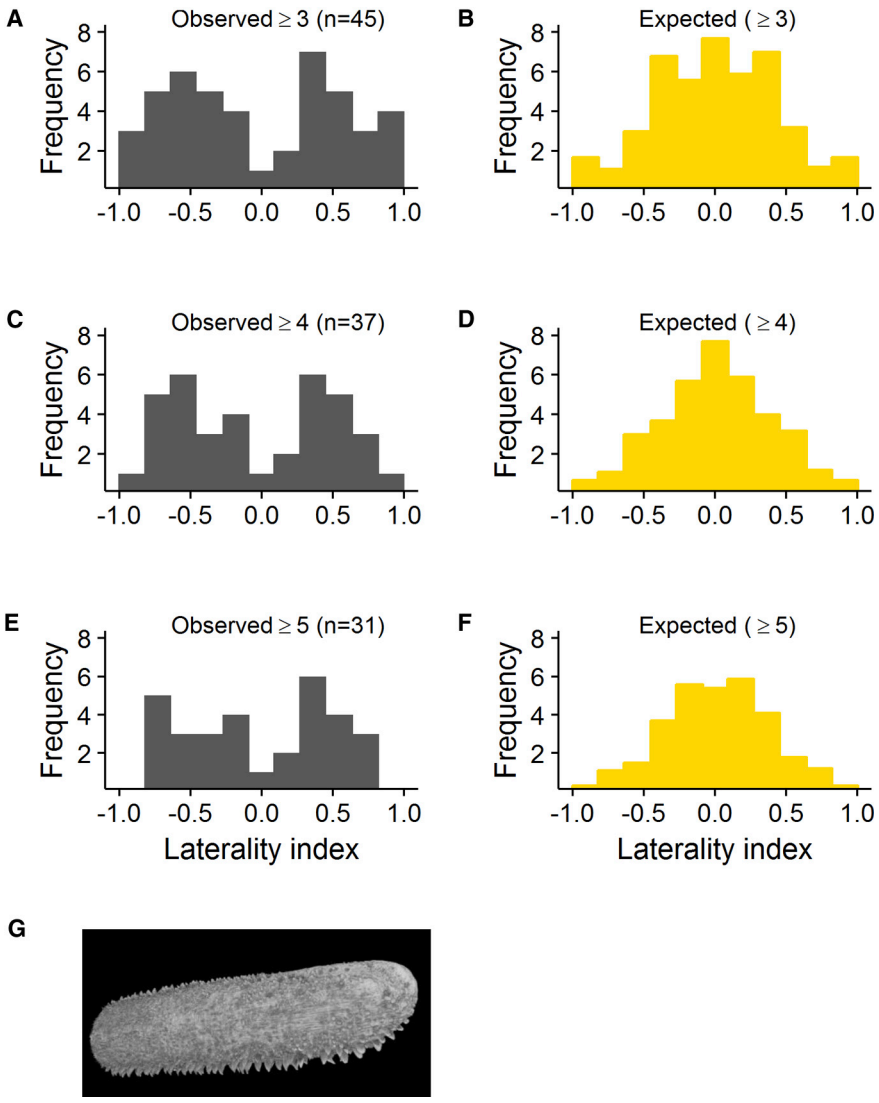

Figure 2. Behavioral and Morphological Evidence for Attack Lateralization in Sailfish

(A–F) The observed (A, C, and E) and expected (B, D, and F) frequency distribution (i.e., assuming no individual-level lateralization) of individuals attacking left or right. A value of −1 corresponds to a sailfish always attacking right, 1 corresponds to always attacking left, and 0 implies an equal number of left and right attacks (i.e., no lateralization). Expected frequency distributions were calculated by assuming a probability of 0.5 for a left or a right attack while keeping the number of sailfish and the number of attacks per sailfish the same, repeating this process 10,000 times. To test the robustness, we used different inclusion criteria, including sailfish for which we observed at least three (A and B), four (C and D), or five (E and F) attacks. n = number of observed sailfish meeting the inclusion criterion. For all comparisons, the observed frequency significantly differed from the expected frequency (all $p < 0.01$). Using the Mclust package in R, we found that for all three different thresholds, the observed laterality index (LI) distributions were best described by a bimodal distribution. See also Figure S1.

(G) Micro-CT image of a 5-cm bill-tip showing the dorsal surface with bill-tip to the right. The micro-teeth are clearly visible on both lateral sides of the bill-tip. On the left side of the bill-tip (upper side in the image) there is an increased micro-teeth abrasion as compared to the right side (lower side in the image). See also Figure S4.

difference in the number of micro-teeth comparing both sides (Figure S4; Figure 2G shows a micro-computed tomography (micro-CT) image of a bill with one-sided abrasion). Using a different threshold for the micro-teeth analysis (e.g., micro-teeth exceeding 0.1 mm) resulted in similar results. This individual-level asymmetry in the number of micro-teeth comparing the left and right side of bill-tips strongly suggests unequal tooth abrasion, providing further support for attack lateralization in sailfish.

Predictability of Attacks

To investigate how sailfish group size affects the group laterality and thus the potential predictability of attacks, we randomly drew groups of different sizes (range: 1–15) from our observed individuals (again, only including sailfish with at least three observed attacks) and calculated the absolute group laterality by averaging the mean laterality of the group members. These analyses show that with increasing sailfish group size, the absolute group predictability rapidly declines (Figure 4). Whereas

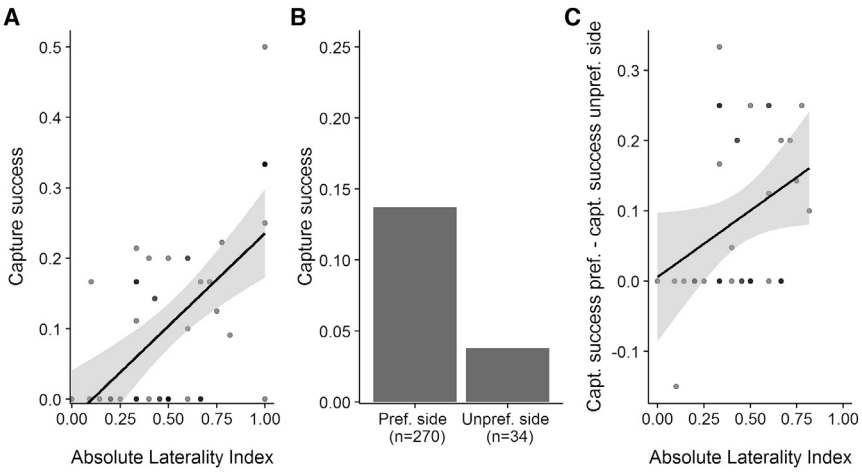

Figure 3. The Consequences of Attack Lateralization on Capture Success

(A) Individuals with a higher LI (i.e., more strongly lateralized) had a higher capture success (i.e., fraction of attacks that resulted in successful prey capture). Each individual dot represents at least one sailfish, with darker dots representing more than one sailfish. Line represents linear regression with 95% confidence intervals.

(B) Sailfish had a higher capture success when using their preferred side than when using their non-preferred side. n = number of observed attacks.

(C) The stronger an individual sailfish was lateralized, the larger the difference in capture success between attacks using the preferred versus non-preferred side. Line is linear regression line with 95% confidence intervals.

See also Figures S2 and S3.

single sailfish are expected to be highly predictable in their directionality of attack (due to individual-level lateralization), larger groups are predicted to rapidly lose their predictability (because there is no population-level lateralization). When comparing this predicted group laterality as a function of group size with the observed group laterality of the 11 sailfish groups (range group size: 1–10), we find that the observed values follow the same trend of decreasing group predictability with increasing group size (Figure 4; Spearman's rho = −0.80, p = 0.003).

DISCUSSION

Our combined behavioral and morphological approach provides strong evidence for attack lateralization in individual sailfish. Importantly, we found no population-level lateralization since the number of sailfish attacking predominantly leftward or rightward was similar (Figures 2 and S3). If one lateralized morph is more common than the other in the population (e.g., right-handedness in humans; [18, 30]), then this would still lead to an overall predictability [3, 17, 21]. In many vertebrates, population-level lateralization has indeed been documented [5, 31], and this has been explained by two opposing selection forces: a need for coordination during cooperative behaviors (selecting for population-level lateralization) and a need for unpredictability during inter-individual agonistic interactions (selecting against population-level lateralization) [21]. In sailfish, the predominant function of the bill is thought to be prey capture [22, 23, 32] and in this scenario, no population-level lateralization is predicted, but rather negative frequency-dependent selection maintaining both types at equal frequency [19]. However, even in the absence of any population-level laterality, individual-level laterality might still be costly for predators whenever a predator repeatedly interacts with the same prey, providing an opportunity for the prey to learn the preferred attack side of a predator. Sailfish, for example, can hunt the same prey group for several hours, which could provide an opportunity for the prey to learn the preferred attack side of sailfish, especially when a sailfish is attacking alone. However, by hunting in a group (consisting of differently lateralized individuals), this potential cost is greatly reduced, especially because sailfish take turns when attacking their prey and individuals only sporadically perform multiple subsequent attacks [23]. By hunting in a group, sailfish can thus maintain the advantages of individual-level lateralization (i.e., increased capture efficiency) while avoiding the costs associated with an increased level of predictability. For this "group-level" unpredictability to arise, a simple random group assortment process is sufficient (given that there is no population-level bias), and it does not require any active dis-assortative mixing by handedness. Future studies could investigate whether predatory groups consisting of a mix of laterality types are more efficient than groups consisting of only one type.

In gregarious prey species, there is mixed evidence for population-level lateralization. In a study comparing 16 taxonomically diverse species of fish [33], species that frequently shoal tended to be lateralized at the population level, whereas species that did not readily form shoals were more likely to be lateralized at the individual level only. This is explained by the increased need for coordination (e.g., during predatory attacks) in more social species. Other studies, however, did not find a population-level lateralization in shoaling species [15, 34]. Whether population-level lateralization evolves into an evolutionary stable strategy as a consequence of social interactions depends on whether lateralized individuals benefit from interacting with similarly lateralized individuals (e.g., coordination) [35]. If, however, there is an advantage of interacting with the opposite type, selection could operate against population-level laterality. In rainbowfish, *Melanotaenia spp*, for example, individuals that showed a right-eye preference for looking at conspecifics in a mirror test were found more often on the left side of the shoal, and fish with a left-eye preference had a slight preference for the right side [36]. Possibly, this could allow shoals consisting of mixed laterality types to more efficiently detect predators and transmit information. How the mix of laterality types in groups affects collective processes is an exciting avenue for future research (see also [37]).

For demonstrating individual-level lateralization in the wild, it is essential to be able to identify individuals. Identifying individuals based on phenotypic appearance is standard practice for

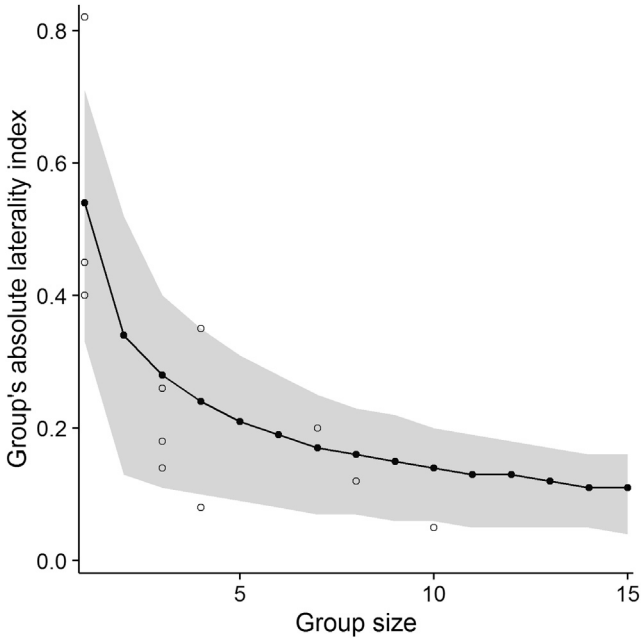

Figure 4. Sailfish Group Size and Collective Attack Predictability

Black line shows the results of simulations investigating the effect of group size on the absolute LI at the group level. Whereas single sailfish are predicted to have a relatively high LI and are thus relatively predictable in their attack direction, the collective LI quickly drops with increasing group size, making individuals in larger groups more unpredictable in terms of attack direction. Simulations are based on randomly drawn groups (10,000 per group size) from our population of sailfish. Gray area indicates interquartile ranges. Open circles indicate observed absolute group laterality of our 11 sailfish groups (only including individuals with at least three attacks) and follow the same downward trend.

several large marine predators such as orcas and humpback whales [38] but a new approach for group-hunting teleost predators. Being able to identify individuals in group hunting marine teleost fishes opens up many exciting avenues for future work for understanding the evolution and dynamics of sociality, including task specialization, producer-scrounger roles, cooperation, and coordination issues.

Generally speaking, there should be strong selection for prey to capitalize on any predatory behavior that might increase survival probability. Sardines are, for example, more maneuverable than sailfish [22], and they might succeed in moving to the non-preferred side of the sailfish bill prior to an attack thereby reducing capture efficiency of predators (see Figure 3B). Future work could investigate this further by studying a wider range of groups consisting of different levels of collective predictability. Future studies could also address the mechanism(s) underlying the increased capture efficiency of highly lateralized individuals. Sailfish rely on rapid bill acceleration for injuring and capturing prey [22]. During such attacks, the entire body performs a rapid bending maneuver, and it is conceivable that strongly lateralized individuals achieve a faster acceleration than weakly lateralized individuals, as hypothesized for C-starts [39]. In scale-eating cichlids, *Perissodus microlepis*, for example, fish attacking with their preferred side showed larger maximum angular velocity and amplitude of body flexion than when attacking with their non-preferred side [40]. Moreover, in shiner perch, *Cymatogaster aggregate*, strongly lateralized fish reacted faster to simulated predation danger and showed higher turning rates than weakly lateralized fish [15].

Conclusions

Using behavioral analyses of identifiable group hunting sailfish, we provide evidence for attack lateralization in individual sailfish. The stronger a sailfish was lateralized, the higher its capture success, due to increased capture efficiency when using its preferred bill side. Morphological analyses of sailfish bills provided further evidence for attack lateralization since most bills showed one-sided tooth abrasion. Single lateralized sailfish are likely to be highly predictable to their prey, which, in turn, can have negative consequences for capture success. However, with increasing sailfish group size, the attacks become highly unpredictable due to the absence of a population-level lateralization. Random group formation is sufficient to reduce collective predictability and individuals do not need to actively associate with oppositely lateralized individuals. We suggest that group hunting may thus favor the evolution of individual-level lateralization since group hunting can offset the negative consequences arising at the individual level. Our work identified reduced predictability as a new benefit for group-living predators and more broadly suggests that group-living predators (at or near the top of the food chain) are expected to evolve greater diversity of behavioral strategies than solitary ones.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and three movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.12.044.

AUTHOR CONTRIBUTIONS

J.K., P.D., and J.F.S. conceived the fieldwork. R.H.J.M.K., J.K., P.D., P.E.V., J.E.H.-R., S.M., J.F.S., M.B.S.S., A.D.M.W., P.C., and K.M.B. performed the fieldwork. R.H.J.M.K., S.K., J.K., and P.E.V. analyzed the data. P.Z. produced micro-CT imaging. R.H.J.M.K. and J.K. wrote the manuscript with substantial input from all other authors.

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